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THE ECOLOGICAL ASPECTS OF SOIL-WATER-PLANT RELATIONSHIPS

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by

Frank Ronco

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INTRODUCTION

Aristotle's theory of plant nutrition and its general acceptance created an early interest in the physiological processes of water and solute absorption from the soil (Kramer, 1949). His theory that the plant's soul, or vital principal, permitted each kind of plant to absorb only the kinds of food proper for its growth was not questioned until the seventeenth century and was generally accepted until the eighteenth century.

The work of Stephen Hales published in 1727 was perhaps the first accepted on the quantitative aspects of plant-water relationships (Kramer, 1949). Since that time, many viewpoints and numerous contributions to our knowledge of physiological processes in plants have been published. That these changes in viewpoints have not been confined to past centuries is pointed out by Kramer who stated that outstanding contributions to our knowledge of cell-water relations were made in the 1920's by several authors. Even within recent years a few physiologists consider themselves vitalists and believe that while living organisms still operate under the laws of chemistry and physics, there are still many phenomena that defy explanation by the application of these laws (Kramer, 1949).

The science of plant physiology as it deals with the internal processes of plants is well established in respect to plant-water relationships. However, the field of soil-plant relationships does not appear to be as firmly entrenched and it is reasonable to suppose that continuing research will provide more information on this subject. Considerable knowledge has accumulated and is continually being amassed in the agricultural sciences. Because of the vast amount of research in farming and crops, better varieties, larger yields, and a wisdom of the interrelationship between various crop plants and their soil habitats have arisen. On the other hand, we do not have sufficient detailed information of this kind upon which we can most efficiently base the management of our wildlands. It is in this field that we can do much to foster a better understanding of the relationship between soils and plants.

Before a discussion of soil-plant relationships is presented, a review of soil-moisture relations and related factors will be presented.

FACTORS AFFECTING THE SUPPLY OF SOIL MOISTURE

Lemmon (1955) has stated: "The productive capacity of a site for timber is related to factors which provide optimum amounts of available moisture for plant growth during the longest period in the growing season." This statement is also applicable to products other than timber, such as other wood products and forage or browse.

The amount of moisture available for plant growth depends upon the amount of precipitation. The effectiveness of this rainfall, in turn, depends upon numerous factors of which the most important will be covered in this section.

Unless otherwise indicated, the information reviewed has been taken from Kramer (1949).

Rainfall

If a large percentage of the precipitation occurs in winter and relatively little in summer, less vegetation will be supported than in regions where heavy precipitation occurs during the growing season. Even though average precipitation during the growing season appears adequate, the distribution may be so erratic that summer droughts often limit plant growth. Summer precipitation occuring in frequent light showers is less effective than heavier rains because of the larger percentage lost by evaporation from light showers. Conversely, downpours are ineffective because of the large percentage of water lost by runoff instead of soaking into the soil.

Evaporation

It has been estimated that in the United States, approximately one-half of the total precipitation is returned to the atmosphere by evaporation and transpiration.

The amount of water vapor lost from the soil depends upon the steepness of the vapor-pressure gradient from soil to air. This, in turn, is affected by both soil and atmospheric factors which for soil, the most important are moisture content and temperature. The principal factors for the atmosphere are temperature and humidity (Kramer, 1949; Lassen, et al., 1952).

Evaporation will be decreased from a soil whose surface is dry because of slow diffusion of water vapor through the dry layer. Experiments have shown that evaporation from soil in contact with a free water table is two to four times as rapid as evaporation from well-drained soils. As a result of misunderstandings from experiments of this type, the advantages of a dust mulch in agriculture has been over-emphasized. It is the general opinion based on later experiments that cultivation does not reduce evaporation to any great extent. Considerable evidence indicates that if the water table is only a few feet below the surface, relatively little upward movement of water occurs. Keen (1928) found very little rise of water in soil cylinders 6 feet high. Under California conditions, most of the water lost by evaporation comes from the upper 4 inches, much less from the second 4 inches, and very little from below 8 inches.

Loss of water by evaporation from the surface layer of soil is probably serious only when much of the precipitation occurs as light rains. Burr (1914) reported that in Nebraska, a rainfall of 0.5 inches or less is entirely dissapated by evaporation unless the surface soil was still moist from previous rains.

Kramer states that while dust mulches seem to be ineffective, mulches of straw, grass, leaves and similar materials are much more effective in reducing water loss. Their greatest benefit is due to shading and subsequent decrease in soil temperature. They also lengthen the diffusion gradient from soil to air and protect the soil surface from drying effects of wind. Russell (1939), however, considers mulches to be effective only in preventing drying of the surface layer, because a layer of dry soil is a better insulator than is the average mulch, and also because it is more impervious to water vapor.

Lassen, et al. (1952) states that soil texture also has an effect on evaporation. Coarse textured soils lose more water vapor and to a greater depth than fine textured soils. He estimates that water in vapor form is lost to a depth of 5 or 6 feet in coarse soils but only to a depth of 1 foot in fine soils. On the other hand, water in liquid form is lost more readily and to a greater depth in fine soils. For sands the depth is about 14 inches, and for clays about 3 to 4 feet.

Kittredge (1954) found that evaporation from the upper 12 inches of shaded mineral soil was reduced to 87 percent of that from bare unshaded soil. However, seasonal differences were noted as shown in the following table:

Season	Soil	Evaporation in forest as percent of open free-water surface
Winter	153	48
Spring	72	37
Summer	60	30
Fall	118	49
Average	87%	41%

It is noted that evaporation from shaded soils exceeded that of open soils during winter and fall. Several possibilities for these discrepancies were offered by Kittredge, but even their sum could not account for the wide variation. As a consequence, no index could be made to compare rate of evaporation from a free-water surface to rate of evaporation from soil. While not conclusive, his data suggests a correlation that an increase of 0.03 inch of evaporation in the forest corresponded to a 0.1 increase in the open.

He found trends of cumulative evaporation from soil after a rain were steep after the first 2-6 days and thereafter increased more slowly at a decelerating rate. Kittredge states that these trends were due to the soil becoming drier; as a result of this drying out the rate of evaporation becomes smaller because less moisture remains to evaporate. There was considerable variation due to the range in evaporation and also to gains of moisture from the atmosphere or deeper layers of soil. Sometimes gain exceeded evaporation but the variations were not consistent. For the entire period after a rain, results of cumulative evaporation data were about equally divded as to deficits and excesses of shaded forest soil compared to open soil. Consequently no statement was made as to the influence of forest on evaporation.

Using the formula, $E = M(1-e^{-kT})$ 1/, Kittredge found that the maximum amount of evaporation (M) that could be expected to occur if sufficient time elapsed tended to decrease with depth. These values of M were usually lower in the forest than in the open. The rate of increase of the evaporation trend (K) were smaller in the upper 2 inches of soil in the forest, but below 4 inches they were larger in the forest than in the open. The values of K did not reflect the influence of the forest consistently. Based on the above formula and other data, Kittredge arrived at the following conclusions:

1. The depth of evaporation decreased with depth below the surface most rapidly in the upper 4 inches of bare soil, and at a decreasing rate downward.

1/ E = the depth of evaporation in inches, M is the maximum evaporation in inches that would occur if the time (T) were sufficiently prolonged. e is the natural logrithm base, 2.718. K is a constant derived from trial and error.

2. The rate of decrease with depth was more rapid in the open than in the forest.
3. Monthly evaporation from 2-inch layers varied from 0.43 inch from the upper 2 inches in the open to 0.02 inch below 16 inches in the forest.
4. About 80 percent of the evaporation from the 20-inch layer in both open and forest came from the upper 12 inches.
5. Fifty percent of the total evaporation from the 20-inch layer came from the upper 4 inches in the open, and from the upper 6 inches in the forest.
6. Daily evaporation decreased as soil moisture decreased.

While many of Kittredge's statements are not statistically significant, they do indicate trends that are important in soil-water-plant relationships. His work also points out the variations and difficulty in obtaining data for this type of correlation study.

The effect of vegetation on moisture in the 10-inch soil layer was studied by Heyward (1939) in longleaf pine (*Pinus palustris*) stands. He found that soil was more moist in unburned stands than in burned stands. Even though the actual difference in moisture percent varied from 1 to 10, the percentage difference was as high as 66 percent. Analysis of his data showed no significant or consistent results due to soil structure or soil particles including organic matter and colloidal mineral fractions. By inference, increased moisture was due to the mulching effect of grass and litter cover and subsequent reduction of evaporation losses which would be higher on burned areas since considerable bare soil is present.

Infiltration

The rate of infiltration is an important factor in determining how much rainfall will be accumulated in soil and how much will be lost by runoff (Kramer, 1949). Infiltration is determined by number and size of non-capillary pores at the soil surface, and any action tending to block these pores reduces the infiltration rate (Lassen, et al., 1952). Compaction, freezing and thawing, and action of raindrops all have the tendency to cause formation of a more impervious surface to rainfall. Formation of such a layer can be avoided and runoff greatly reduced by crop cover, mulches, and by incorporation of organic matter into the surface of soil (Kramer, 1949).

While incorporation of organic matter into surface soil is important for infiltration it also has significance from an ecological standpoint. Since this paper is primarily concerned with soil-plant relationships, perhaps it would be appropriate at this time to discuss the importance of the ecological problem of the humus layers in the forest. The following discussion of mull and mor types of humus is taken from Romell (1935). Mull is ecologically richer both in species and number of nitrate plants which are absent on mors. Most of the northeast American hardwood species either require or are favored silviculturally by mull, whereas most conifers may be unfavorably affected by mull soils. However, white pine (*Pinus strobus*) may give better production on mull soils. In the United States, mulls are associated with brown forest soils in the northeast, whereas mors are associated with conifers.

Composition of the stand, thinnings, green slash, clear cutting, light burning, ripping of mor cover, or liming may activate a mor by starting nitrification and bringing about a mull like humus. They may even cause conversion of a mor to a true mull. Generally this activation occurs in intermediate climatic regions, but it has been known to occur in mor climates where more drastic measures may be required to start the activation process. Romell states that in some instances, eg., the Black Forest in Germany, clear cutting may bring about a worse mor condition.

Ecological differences between the two types of humus are due to action of bacteria in mulls and fungi in mors. Some fungi in destroying lignin and/or cellulose compounds produce acids either by direct decomposition or by activity of the organisms. Bacteria on the other hand, do not cause formation of acids. The activity of bacteria tend to inhibit growth or increase of acid forming fungi, which because of their nature usually increase to the point of mor conditions once established.

The fact that mull soils are higher in nitrogen is due more to distribution and type of micro-organism than to rate of decomposition of organic matter caused by the organism. Roots and fungal mycelia are more concentrated in a mor and remove more nitrogen than roots and bacteria which are spread out over a larger area in the mull, thus removing less nitrogen.

Romell has shown that mor samples have an increased amount of mobilized nitrogen for two reasons: First, reduced competition for nitrogen as a result of fungal hyphae being broken and killed, and second, dead hyphae release nitrogen to soil much as a green manure. Any forest practice which aids in setting up the above conditions enhances activity of nitrogen formation and lower fungi population, and provides conditions more favorable for mull formation.

Percolation

As was mentioned previously, infiltration will to some extent determine the effectiveness of rainfall, but once water has penetrated the surface it must be removed by percolation into deeper soil horizons before any additional infiltration will take place. Rate of water movement through soil is dependent upon the characteristics of the soil, chief of which are texture, structure, kind of clay minerals present and kind and amount of exchangeable ions absorbed upon them, and amount of organic matter incorporated with mineral matter (Kramer, 1949). All of these factors have the function of regulating or determining the amount of air volume or pore space. That portion of pore space composed of large pores, macropores, from which water drains by gravity and which is therefore normally filled with air is termed non-capillary porosity to distinguish it from that part of pore space which is normally filled with capillary water. Baver (1948) states that an ideal soil has pore space about equally divided between large and small pores. Such a soil has enough large pores to permit adequate drainage and enough small pores to give adequate water-holding capacity.

Lassen, et al. (1952) states that retention storage of a soil is affected by organic matter, which increases water holding capacity of soil particles as well as total volume of the soil. It can absorb 4.4 times its own weight of water. When decomposed it clings to soil particles and coats them with a gel-like porous substance which increases their surface area. Incorporation of decomposed organic matter into soil may increase or decrease retention storage capacity per unit volume of soil depending on the amount of organic matter originally found in the soil. For soils with an organic matter content of less than 5 percent, any addition will increase surface area and holding capacity, but volume and number of soil particles per unit volume will remain unchanged. As organic matter increases above 5 percent, volume weight or number of particles per unit volume decreases. With fewer particles per unit volume less surface is available for water absorption. This means that even though storage capacity of individual particles is increased, capacity per unit volume of soil may be reduced. Thus, compacted soils or soils low in organic matter may have more storage capacity per unit volume than similar soils with high organic matter content.

Inversely proportional to the amount of water retained by soils is the amount of air present in soil pores. Romell (1922) observed that poor aeration in soil is due primarily to water, since high values of oxygen deficiency were found only in wet soils. He states that oxygen deficiency in soil air is determined by intensity of oxygen utilizing processes and rate of gas exchange between soil and air. The oxygen utilizing processes are affected by amount of decomposing organic matter in the soil, and organisms acting on this organic material. Rate of diffusion is about the same over a wide range of soil textures, but is considerably retarded in heavier clay soils. Romell concludes that rate of diffusion is normally of sufficient magnitude to provide for proper aeration of most forest soils.

As with infiltration, any activity tending to cause a reduction in number of large pores will reduce percolation. Compaction influences percolation directly by decreasing pore size and indirectly by hindering root development (Lassen, et al., 1952). Where soils have less than 5 percent non-capillary pore space, root penetration is severely decreased if not stopped entirely. It is difficult to measure the quantitative influence of roots on percolation, but Lassen states that root-soil interfaces as well as cavities left by dead roots provide avenues for downward movement of water.

Root development depends upon its hereditary aspects and on such environmental factors as soil texture, structure, moisture content, aeration and temperature; kind and concentration of solutes; and competition with other roots. Hellmers, et al. (1955) in a study of chaparral plants found that roots frequently changed direction in response to hard soil or other obstacles. Occasionally, roots grew in one direction for several feet only to turn back. The authors recorded one instance where a chamise root (*Adenostoma fasciculatum*) extended downward for 2 feet, reversed direction, grew upward to within a few inches of the surface and less than a foot from where it had started, and then grew horizontally to become a major lateral root.

Since root penetration does depend to a great extent on porosity, Auten (1933) posed the question as to the depth porosity extends downward from the surface. His studies in the central states on old growth forest soils and field soils showed that the former were 15.3 percent lighter than field soils in the upper 9 inches of soil profile. However, porosity as determined by volume weight was not uniform in each of the soils as depth increased. In the upper 0.3 inch depth, field soils were 43 percent heavier; in the 3-6 inch depth, field soils were 12 percent heavier; and no difference between soils was observed in the 6-9 inch depth, but water absorption capacity was greater under forest soils. Relative ratios of water absorption at the 1-inch, 3-inch, and 8-inch depths in forest and field soils was 205 to 4, 72 to 5, and 9 to 4. He concludes that porosity differences are due more to soil structure than organic matter, because of the small difference between real specific gravity (2.613) for forest soils and (2.623) for field soils. It appears that Auten's conclusion is untenable with that of other authors who found that organic matter and structure are very closely related. Lassen, et al. (1952) effectively sums these viewpoints by stating that non-capillary storage is increased by addition of organic matter to soils. It acts as a separator and binding agent for soil particles thus increasing pore size. Total porosity is increased, but capillary porosity may be reduced in some instances.

Severe burning may also have a detrimental affect on soil structure and porosity. Dyrness and Youngberg (1957) found that clear cutting and burning of slash caused a reduction in percent of silt and clay fraction caused by dehydration and subsequent fusion into secondary sand particles. This effect was not noticed, however, in loam soils which actually increased in silt content. They also found that organic matter was decreased by 61 percent and aggregation by 21 percent. The decrease in the latter was due to fusion of finer fractions into sand at the surface 1/2 inch, and oxidation of organic cementing material to a depth of about 2 inches.

CORRELATIONS BETWEEN LAND USES AND SOIL CHARACTERISTICS

Trimble, et al. (1951) in a detailed study of the Allegheny River watershed attempted to determine rates of water movement and storage capacities of various soil profiles, and effects of soil, cover and land use on these water conditions. The soil-cover-use complexes were grouped on the basis of the most important and most variable soil-water value, percolation rate. Values were determined for detention storage, retention storage, organic matter and volume weight for each significant percolation class. Because of inadequate sampling, no conclusions could be drawn from analysis of the percolation data for woodlands which were not grouped. However, when grouped to form an ungrazed woodland complex significant differences were noted.

The humus type in this complex was selected as the basic indicator of cover conditions. Of the five types of humus in ungrazed woods, only mors, firm mulls and other mulls (coarse, medium, and fine mulls) were found to be significant. Percolation rates in the A_1 layer of "other" mulls and H layers of mors are sufficiently high that any rainfall intensity should not exceed them. No difference in percolation rates could be detected in the lower A horizon of mors and the lower A horizon in mulls. The authors attributed this condition to high organic matter and weak leaching in this horizon of mors. Percolation rates in humus were reduced in grazed woodlands, but inadequate sampling could not differentiate between degrees of grazing. Grazing also reduced organic matter 32 percent, and increased volume weight 80 percent in the humus layer. No correlation could be made between percolation rates and age and density of the stand. The samples, though insufficient, did indicate that in a profile below a humus layer any difference due to stocking and age develop slowly. In general, soil-cover complexes that increase percolation rate also tend to increase the volume of detention storage. The authors found that in general, regardless of vegetative cover, open land soils had less percolation and detention than forest soils in the upper horizon. Smaller differences were noted in the B horizon, and no difference in the C horizon. However, their studies did not take into consideration the influence of large roots on water movement. Retention storage was not affected by grazing in woodlands, and it remained the same for both forest and openland soils for comparable horizons. They attributed this to the high colloidal content of the loam and silt loams to which organic matter can add little in the way of retention storage.

Trimble and his co-authors also found a fairly close correlation between volume weights and organic matter content. A similar relationship was also noted between detention storage and volume weight. In summary, the study shows that better land management practices affect greater results in upper soil horizons. Indirectly these practices affect other horizons in that it may make lower horizons capable of utilizing their full detention and percolation capacities.

Similar results were also obtained by Auten (1933) who found, in comparing open fields to plantations, an increase of 13 percent in volume weight of field soils. Furthermore, the age of plantations is not critical, since soil became more porous as soon as the plantations became established. He also observed that porosity is obtained more quickly in conifer plantations than in hardwood plantations. The ratios of absorption at the 1-inch depth were 100 cc/min. for plantations, and 8 cc/min. for open fields. The absorption at the 8-inch depth were 13 cc and 3 cc/min. respectively, showing that factors influencing absorption are more active in the surface layers. He concludes that the problem of forest soils is inseparably connected with forests, which in turn are inseparably connected with good silvicultural practices.

SOIL-WATER-PLANT RELATIONSHIPS ON AN ECOLOGICAL BASIS

The early pioneer settlers of America recognized the relationship of forest vegetation and soils. They considered "'white pine soils' as fair pasture, 'Norway pine soils' as mediocre fields, and 'jack pine soils' as soils unsuited for agricultural use" (Wilde, 1958). According to Wilde, the knowledge of these people was used by early ecologists as the basis for broad generalizations and classification systems that had very little backing in authoritative evidence. Later students of ecology and forest soils learned that the influence of soil properties is altered by climatic factors and forest vegetation.

A striking example of this influence is exhibited by white oak (Quercus alba) found on upland silt loams from western Minnesota to southern Indiana. Near the drier western portion the stands are savannah-like with scraggly trees yielding about 4 cords per acre. With improved conditions near the Iowa-Wisconsin-Illinois boundary, white oak attains fair dimensions yielding about 12 m board feet per acre. In the mild environment of the Indiana hills, volumes of 40 m board feet per acre are reached in the form of nearly cylindrical veneer logs.

Coile (1952) states that the relationship between soil and forest vegetation is not always discernable by observation, but may only be revealed by detailed soil analyses, rate of growth, or quality of timber. Some of the more obvious relationships are exemplified by jack pine (Pinus banksiana) or Scotch pine (P. sylvestris) on sandy soils, hard maples (Acer saccharum and A. nigrum) or basswood (Tilia spp.) on fine textured soils, and alder (Alnus spp.) on muck or wet soils.

Other species occur on soils which vary greatly in their texture, drainage, and fertility (Wilde, 1958). Both white pine (Pinus strobus) and aspen (Populus tremuloides) are found on coarse to fine textured soils, well to poorly drained soils, and on soils rich or poor in nutrients. However, optimum growth of these species depends upon a balanced supply of water, air, and nutrients. Moreover, the form of stems, crowns, and root systems of nearly all tree species are altered when grown on different soils. Hilgard (1906) describes as many as four morphological varieties of post oak (Quercus stellata) and black oak (Quercus velutina) when grown on upland loams, sandy ridges, flatwoods, and prairie soils of the south.

The influence of soil properties on vegetation may be altered by "mass action of the forest" (Wilde, 1958). According to Wilde, the occurrence of a tree species on a certain soil type depends to some extent on composition of the surrounding forest cover and on size of the soil area. A few acres of loam on clay soil in a region of sandy deposits occupied by pines often do not support exacting hardwoods, because the pines form a barrier against intrusion of other species. In addition to the physical barrier, a biological hinderance may be caused by unfavorable forms of humus, high incidence of damping-off fungi, or the presence of fauna unfavorable to establishment of invading species. Wilde also states that these barriers have a very important influence in the distribution of trees and ground cover plants. For example, he believes that the northwestern boundary of hemlock (Tsuga canadensis) is established by a combination of biotic factors and not by climate and soil.

Soil characteristics, especially moisture regime, will often determine not only the productive capacity of a soil, but also the distribution of species on that particular soil. Roe (1935), working in the Lake States in areas where soil surveys were not available, assumed that since different soils have the same cover, the limiting factor is soil moisture conditions. He based moisture relationships on texture of surface soil, characteristics of subsoil, and soil moisture expressed in relative terms from dry to saturated. The texture varied from sandy to peats and mucks.

Roe observed that jack pine was found not only on dry soils, but on soils having more moisture but with a sandy subsoil indicative of dryer conditions. Oak was generally found on more moist sites than pine. Soils with an intermediate moisture range have a cover of northern hardwoods in the hardwood climax region; whereas, in the fir-spruce climax region soils should be occupied by white spruce (Picea glauca) and balsam fir (Abies balsamea). However, this was not the case, since hardwoods were more abundant. The author attributed this discrepancy to either inadequate sampling or fire making the hardwood more abundant relatively. Excessively wet soils in the south had a cover of bottomland hardwoods, while in the north the cover was coniferous swamp. In summary, as soil changes from dry to fresh to moist, the cover changes from pine to oak to the climax northern hardwood or spruce-balsam. On the opposite side of the moisture regime, when soil changes from very wet to wet to moist the cover changes from coniferous swamp to bottomland hardwoods to the climax of spruce-balsam or northern hardwoods.

Roe also found a definite correlation of forest types and soil types in areas having soil surveys. From his data he derived the following conclusions:

1. Jack pine is found on sandy soils.
2. Pine and oak equally dominant are found on soils somewhat heavier than pine soils.
3. Oak soils were found to be more variable, varying from sands to silt loams.
4. The northern-hardwood type was generally found on loams, fine sandy loams and silt loams.
5. The white spruce-balsam fir type was mostly on heavy loams.
6. Bottomland hardwoods were not limited to any exclusive soil type. The presence of the type was probably related to an abundant water supply such as a high water table.

Roe listed many exceptions to the above generalizations, which he attributed to the same name being used for soils not having identical characteristics, experimental error, and difficulties in mapping and surveying some of the areas because of topography.

Roe attempted to relate site quality (as an expression of growth) to soil types, but the degree of correlation was not as high as that for cover versus soil. Although a significant correlation did occur between the site index of 5 type species and soil types, no general statement could be made concerning the relation of site quality to soil texture except for one type species - aspen. Sands and light loams are poor sites for aspen, whereas loams and heavy loams are good sites. The other type species as listed by Roe, were jack pine, sugar maple (Acer saccharum), oak spp., and white pine.

Roe also found differences between broad soil groups (as used in the cover versus soil correlation) and site quality were significant. Aspen again showed the best correlation. Poor sites were those which had sandy or mucky textures and were either wet or dry. Good sites were moist surface soils with a clay subsoil. In general, the other species showed more or less the same relationship; dry soils are poor sites for all species; fresh and moist soils are generally good to medium sites; and wetter soils are usually medium to poor sites, except for the two pine types where the soils are considered to be good sites.

Roe states that such information would be useful for determining:

1. The species to plant in reforestation.
2. Type conversion.
3. Land acquisition.
4. The productivity of soil groups for a specific type, or relative production of one species to another providing

> they are both suitable to the same soil type or soil group.

A survey of a Wisconsin catena by Wilde and Leaf (1955) showed a close degree of correlation between differentiated soil profiles and composition and density of ground cover. Five soil profiles were recognized within a distance of 600 feet from a moss-peat bog. Closest was a sandy gley podzol, followed at increasing distances by a sandy podzol, podzolic sand, weakly podzolized sand, and melanized sand. The density and frequency of important indicator plants was greatest and was limited to one or more adjacent members of the soil catena.

(Ceanothus ovatus) and (Arctostaphylos uva-ursi) were limited to a melanized sand.

(Maianthemum canadense) was abundant on podzolized sand. More plants of (Gaylussacia baccata) were found on a sandy gley podzol, but some occurred on podzolized sand and sandy podzol. (Gaultheria procumbens) was equally abundant on sandy podzol and sandy gley podzol, whereas (Cornus canadensis) was limited to the sandy gley podzol.

Tarrant (1953) concluded that soil moisture as affected by poor drainage and high water table is responsible for extensive stands of lodgepole pine (Pinus contorta) in the ponderosa pine (P. ponderosa) zone of Oregon. The adaptability of lodgepole to these poorly drained sites is due to its ability to produce a more lateral type of root system. Where drainage is intermediate, both species may occur in equal abundance. When both species happen to be present on well drained sites, the more rapid growing ponderosa usually overtops lodgepole.

A study by Fraser (1954) related distribution, growth and condition of trees to environmental conditions as reflected by soil moisture. For his investigation he divided the soil moisture regime into 11 units according to soil profile development. These units were indicated by indices θ (Theta), and 0 to 9, where theta indicates excessive drainage and 9 refers to soils that are so wet that little or no leaching occurs. The climatic climax expressed by temperature and moisture occurs at index 2. According to Fraser, the depth of the water table as affected by run-off, seepage, and rainfall, determines the moisture regime.

Only moisture regimes 1 to 6 were found on the study plot, but reconnaissance studies were made to establish the occurrence of tree species over the entire range of soil moisture conditions. The latter will not be discussed in this paper. The climax species yellow birch (*Betula lutea*), sugar maple, beech (*Fagus grandifolia*), and hemlock occurred on all moisture regimes of the study plot. However, each species showed a preference for certain sites as indicated by their abundance and basal area. Yellow birch was partial to moisture regimes 5-6. Sugar maple and beech showed a reverse trend with greatest abundance occurring on moisture regimes 1-2. Hemlock was most abundant on the intermediate moisture regime 3. Red oak (*Quercus rubra*) and white birch (*Betula papyrifera*) were restricted to drier sites (1-3) whereas black ash (*Fraxinus nigra*) occurred only on sites of moisture regimes 4-6. Several other tree species were present, but were not well enough represented to draw any conclusions.

While soil moisture is in many instances a determining factor in tree growth and distribution, other factors operating independently, but capable of influencing soil moisture, may also be a limiting factor. For example, Scholz (1937) found that soil texture influenced growth of red oak and chestnut oak (Q. montana). Both species made more rapid growth on clay loam soils than on heavy clay loam or clay soils. However, prediction of site index based upon soil texture was not possible because two areas having soil with the same mechanical composition may be very much different in respect to other physical factors such as exposure, slope, depth of litter, moisture content, etc.

A study by Livingston (1949) provided information on the causes permitting establishment and survival of a forest community in a region where the climax is mixed prairie. His study concurs with that of Williams and Holch (1946) who concluded that climatic factors were not responsible for the migration of ponderosa pine onto the plains or its zonation. They suggested that soil factors were the primary causal agent.

Livingston's data showed that while rainfall, temperature, and evaporation influence distribution of ponderosa pine they are least important of the interrelated factors. His data also noted that forest was consistently found on coarse textured soil and grassland on finer textured soil. In addition, forest soils were underlain by impermeable conglomerate rock at depths of about 3 feet, which was responsible for a mat-like layer of roots just above this substrate. Because of this layer of roots, Livingston concludes that during periods of high rainfall, moisture concentrates above this conglomerate in the form of a suspended water table and is probably available for a long period of time. This condition and the lower moisture equivalent, lower wilting percentage, reduced runoff, and more rapid infiltration of the coarse textured soils produce a more mesic sites which permit development and maintenance of the arborescent community.

Billings (1950) offered another explanation for the presence of a post-climax stand of ponderosa pine and Jeffry pine (Pinus jeffreyi) in the Great Basin area east of the Sierra Nevadas. The climatic type vegetation in this area consists of sagebrush or pinyon-juniper. Rather than physical soil properties being the causal agent, Billings found that chemical factors were responsible for the pine vegetation. In every case, the presence of the montane species was on hydrothermally altered andesite, which is highly acidic and very deficient in exchangeable bases, phosphorous, and nitrogen as compared to soils developed from unaltered rocks of the same type. The pines apparently are adapted to low concentrations of nutritional elements; however, this may be compensated by the utilization of minerals in the less weathered rock by the deeply penetrating root system. The importance of the low mineral content is reflected by the inability of sagebrush herbs and grasses to survive and grow normally on these altered rocks. Consequently their absence allows soil moisture to be utilized by pines which are then capable of surviving in a region where the climatic vegetation is sagebrush.

Billings concludes that the pine stands are remnants of a more moist period and whose continued presence is due to the inability of sagebrush and its associates to invade these mineral deficient soils.

The studies of various authors up to this point have dwelt primarily on the relationship of climax vegetation and soil. This phase of soil-plant affinities is by no means the entire picture as may have been inferred from the work of Auten (1933) cited in the previous section. That there is a change in the vegetation from abandoned fields to a climax forest cover and that each of these subclimax types affects a change in soil characteristics which may be causal factors in the development of succeeding stages, has been implied by most ecologists. Aside from changes in soil characteristics that tend to reduce water loss, perhaps a greater effect of plant cover in successional stages is decreased soil erosion. Warner and Aikman (1943) studied five secondary successional stages from bare soil to maple-linden climax in central Iowa, and found that soil losses were reduced about 96 percent on the climax stage. According to the authors, this indicated a definite relationship between soil building properties of vegetational stages and soil losses.

One study dealing with changes in soil characteristics and the subsequent affect on the following climatic stage was performed by Coile (1940) in the Duke Forest near Durham, North Carolina. His work dealt with successional changes from abandoned fields to loblolly pine (Pinus taeda) to the white oak-black oak-red oak climax forest. Pine may become established any time after field abandonment providing adequate seed supply and weather conditions are favorable. Because of this ability of loblolly to become established immediately, a change in soil characteristics is not necessary for establishment.

Oaks and hickories which are dominant in the climax forest do not become conspicuous in the reproduction layer of pine stands until the latter are 20 to 40 years old. Coile states that effects of a soil change may be a causal factor in the invasion of climax species. By the time the climax species began to appear in abundance, an A_0 horizon has formed which favors acorn and hickory nut storage and germination by reducing water loss during storage. On the other hand, the presence of this horizon has a detrimental effect on pine germination because the light seed remain on top of the litter where insufficient moisture is available for germination and survival.

Coile found that the following soil characteristics were probably not a cause of the hardwood invasion: carbon-nitrogen relations, available nitrogen, exchangeable calcium, field percolation rates, volume weight, air space, and water holding capacity. In fact, the first three items indicated that more available nitrogen is probably present in land recently abandoned than in pine stands 20 to 40 years old. He also noted that volume weight, air space, and water holding capacity change but little during succession. It was surprising to note that percolation rates decreased with invasion and early dominance of loblolly pine. This was attributed to the disappearance of old-field lesser vegetation, namely broomsedge (Andropogon spp.) which annually added deeply incorporated organic matter to the soil of abandoned land through death of roots. The highest percolation rates were found in pine stands 50 to 100 years old, after which time percolation decreased even in the climax oak forest. This condition was due to better mixing of organic matter in the A_0 and A_1 horizons of pine stands, whereas the humus in the climax forest was more mat-like.

Coile also pointed out that lack of pine reproduction was not due to any soil changes, but was caused by morphological characteristics. The shallow rooting pine is not able to penetrate the first few inches of soil surface rapidly enough to enter more moist soil. An additional factor aggravating this condition is the concentration of small roots in surface soil. The number of these roots increases as succession increases, and becomes greatest in the climax forest. Climax species on the other hand, are able to put down a deep tap root soon after germination, and thus have a well developed root system below the zone of moisture stress.

Many investigators have compared the effects of vegetation on the physical and chemical properties of soils. Mergen and Malcolm (1955) studied the influence of hemlock (Tsuga canadensis) and red pine (Pinus resinosa) on certain soil properties in two soil types. These properties included volume-weight, pore volume, field capacity, air capacity, infiltration rate, pH, and calcium content. They found that in plantation I on sandy loam the only difference between the surface soil under the two species was a slightly lower pH value beneath hemlock than beneath red pine. However, in plantation II on loamy sand, there was no difference in the pH value. Calcium content in plantation II was considerably greater under hemlock than under red pine. Wilde, et al. (1937) also found a higher replaceable calcium content beneath hemlock stands as compared to red pine stands. Despite differences in calcium content in the A_1 horizon under hemlock and red pine, there was no difference in their pH values. The authors found no relationship between pH values and calcium content. Plice (1934) in a study of chemical properties of tree litter, also found no consistent relation between base content, antacid buffering, and acidity of litter of a large number of tree species including red pine and hemlock.

Other investigators also found differences in chemical behavior of litter of different tree species. A comparison of surface soils beneath stands of eastern red cedar (Juniperus virginiana) and red pine showed that calcium content and pH values were higher in the A horizon beneath eastern red cedar than under red pine (Read and Walker, 1950). Alway, et al. (1933) investigated chemical properties of unincorporated organic matter on soils under red pine, jack pine, white pine, and sugar maple-basswood types in Minnesota. They found that differences in ash, lime, nitrogen content, and pH values in these organic layers were small between jack and red pine, but large between these pines and the maple-basswood type. Plice (1934) also studied the content of calcium and other bases, antacid buffering, acidity and total nitrogen content of leaf litter of several coniferous and deciduous trees on various soils in northeastern United States. There were differences in these chemical properties between species, and some variation within species on different soils. He also observed an influence of tree cover on properties of litter and humus layers of soil.

Mergen and Malcolm found no differences in physical properties of surface soil under the two species in plantation I. They attributed this to lack of earthworms whose presence was prohibited by raw humus and low calcium content of unincorporated organic matter and surface soil. Read and Walker also observed lack of earthworms in soil with a low calcium content. Plantation II had a higher pore volume and faster infiltration rate beneath hemlock. This was attributed to higher calcium content which was indirectly beneficial by causing soil to flocculate and the subsequent binding together of these floccules by organic matter. Calcium is also conducive to the presence of micro-organisms which incorporate organic matter into the A horizon. As a result of their study, the authors found no evidence to show that red pine is preferable to hemlock in regards to the maintenance of soil fertility.

SITE QUALITY BASED ON SOIL CHARACTERISTICS

One of the ultimate objectives or applications of soil-plant relationships is the evaluation of site for tree growth and production. Numerous investigators have used site index and plant indicators as a measure of site quality; however, as Gaines (1949) points out in his review of literature, both of these methods have definite limitations and are not entirely satisfactory. Other investigators have used soil characteristics to evaluate site quality, approaching the problem from either the chemical or physical properties of the soil. McClurkin (1953) states that most of the usable correlations have come from a comparison of physical properties. Gaines concurs with the above statement, but goes on to say that nutritional or chemical factors may be important in some regions or under certain conditions in any region. Both Gaines and Coile (1952) present excellent reviews pertinent to soil characteristics and site quality.

Gaines lists the methods used by some authors for classifying sites from soil factors. Each of the systems has in common certain soil factors, but there is also disagreement on other factors that should or should not be considered, depending upon the author's views. As Gaines points out, "The exact factors to be used will undoubtedly vary widely from one region or type to another. In some regions the relative stability of soil factors, or the ease with which site may be degraded or rehabilitated, may be of considerable importance; in other regions it may be of little importance. The purpose of the evaluation must be considered, for different factors are more important in regeneration and early growth of trees than in later growth and development, and different species have different requirements throughout their life."

Any system used, should have the quality of easily measured factors in order to be most workable and applicable to field use. It is not the intent of this paper to discuss the various systems of site quality versus soil characteristics or the ramifications thereof. Only one example will be given of what appears to be a workable and simple scheme for use in one area of the United States. There is no reason to doubt that the system may also be applicable elsewhere. McClurkin (1953) showed that in the Gulf Coastal Plain region longleaf pine site quality can be predicted from rainfall and the depth of the soil to the least permeable horizon. He found that as rainfall and soil depth to the least permeable horizon increase, the site index also increases.

SUMMARY

The management of land requires a knowledge of the relationship between soils and plants. Soils will affect plants, which in turn will affect the soils upon which they are grown. This review of literature places emphasis on the affect of soils on plants, however, following this approach is somewhat difficult because vegetational influences may alter the soil characteristics. As a consequence, a new set of soil factors are initiated which may change the quality or quantity of the biota. Successional stages from bare ground to the climax vegetation in a given region best illustrate this principle.

Within a soil-plant-water relationship, the amount of soil moisture appears to be the critical factor in nearly all instances. Evaporation, infiltration, and percolation will determine the amount of water in the soil after the initial wetting by precipitation. These processes in turn are influenced by temperature, humidity, and such soil characteristics as texture, structure, organic matter and chemical content, and the presence of roots and micro-organisms. Land uses and vegetation will also exert their influence on the soil moisture content.

As a result of the total effect of these many factors, a soil moisture regime is initiated. The establishment and survival of a species on any particular regime are limited by the inherent characteristics of these species. A few studies concerned with this phase of soil-water-plant relationships have been presented in this paper; however, there are many more.

A knowledge of the many interrelationships is necessary for the proper management of forest lands. This information could be applied to such management problems as reforestation, afforestation, type conversion, land acquisition, and site productivity or quality.

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